MORPHOLOGIC SEQUENCES IN THE CANALICULATE FULGURS.

BY BURNETT SMITH.

The Tertiary and Recent gastropods which are usually assigned to the genus *Fulgur* or to the genera *Fulgur* and *Sycotypus* have been studied on several occasions in the endeavor to clear up the phylogenetic relationships of the different species. Inexact methods of collecting, poorly preserved material, and uncertainty of stratigraphic relations have perhaps contributed in no small degree to the conflicting interpretations which have resulted. In spite of the attention which these forms have attracted, no detailed morphologic work has, so far, been attempted in the group. The purpose of the present paper is to record some of the changes exhibited by the canaliculate division of the genus when traced throughout its geological and geographical range.

The following notes have been prepared after an examination of well-preserved specimens whose localities and horizons are in most cases known to have been determined with considerable accuracy. Museum sets of individuals falling well within a single specific diagnosis have been omitted whenever there was a suspicion that they were derived from more than one locality or from more than one horizon. It is recognized, however, that the amount of collecting necessary for a final settlement of these problems of phylogeny is far beyond the resources and the time of any one individual. Conclusions reached in these notes are therefore submitted with the full realization that they are preliminary in character and limited in scope.

In even so simple a structure as the gastropod shell there are too many features to be taken in and appreciated at a single glance, and when a number of gradational forms are viewed together it is seldom possible to retain any definite mental image in passing from one extreme to the other of a morphologic sequence. True, it can be seen by the most casual inspection that many species are closely allied, but to say *how* they are allied is by no means an easy matter. The chief obstacles encountered in such work are those presented (1) by multiplicity of morphologic characters, (2) by the inadequacy of words to express the requisite shades of meaning, and (3) by the difficulty of representing a transitional ontogenetic stage in a diagram.

In spite of their shortcomings it is believed that diagrams give a closer approximation to the truth than verbal descriptions and can be employed to greater advantage if their limitations are understood.

Though fully appreciating the necessity for the correct use of systematic terms, the author wishes to emphasize the point that the present study has not for its object the comparison of species as ordinarily understood, but the comparison and correlation of the morphologic combinations exhibited by the majority of individuals of communities or races.

Wherever practicable, the forms examined have been compared with type specimens. When this could not be done satisfactorily it has been the policy to refer, if possible, to some good figure of a specimen whose horizon and locality are known. Though this latter method may perhaps increase the chances of confusion among names, it is believed that it lessens the chances of confusing morphologic units.

In the group of gastropods under discussion the shell characters most available for comparison are the sutural canal, the nodes on the shoulder angle, and the shoulder-angle keel. The appearance and disappearance, strength or weakness, persistence or the reverse of these characters have been used in comparing one race or species with another. Decortication in many fossils and mechanical abrasion in most recent specimens have usually obscured the minute details of the first and second whorls. It is therefore not possible to compare here every ontogenetic stage, but it can be stated that the sequence of ontogenetic stages for the group appears to be (1) a smooth and rounded stage, (2) a short cancellated and rounded stage, (3) an angulated and noded stage, (4) an angulated and keeled stage without nodes, and (5) a final rounded stage in which only the faintest spiral striæ remain.

In the present study, as mentioned above, the last three stages are, together with the canal, the most useful for comparative purposes. It is unfortunate that it is not practicable to extend the comparisons in detail to the first and second whorls, but the nodes are usually much obscured on the second whorl, while the cancellated stage is known to the author in only one fossil race. Its presence, though not proved, is suspected nevertheless for the entire group of canaliculate Fulgurs.

In order to restrict, as far as possible, the verbal description of each feature in each whorl of each race, it is deemed advisable to present the diagrams first and allow them to serve as a guide to the

explanations that may follow. The purpose of the diagram is to picture the persistence or the reverse of the different characters in passing from the early to the late whorls, that is, throughout the ontogeny of the average individual[1] of a race. The heavy horizontal line of the diagram represents the ontogeny. It might be described as a linear representation of that which in the shell is spiral:—the spiral shell unwound, if we may use such an expression. Above this line the ontogenetic stages are marked off as follows:

A. The smooth and rounded stage.[2]
N. The noded stage.
K. The keeled stage without well defined nodes.
R. The final rounded stage.

The ontogenetic range of the sutural canal is shown below the heavy line mentioned. The vertical dotted lines delimit the different whorls and the spaces between them are numbered accordingly.

It has been found by measurement that (due to ventricose coiling) the length of the shoulder on any one whorl is about twice as great as that on the preceding whorl. This, though not mathematically correct, is believed to be so close an approximation to the truth that the diagrams can be constructed in this manner. Whorl seven is accordingly shown as twice as long as whorl six, and this proportion is maintained down to the third whorl. (See tables on p. 570.)

The Coronatum-pyrum Sequence.

The sutural canal or channel which is such a prominent character in our two Recent species of canaliculate Fulgurs and which is usually selected as the chief diagnostic feature of the genus or subgenus *Sycotypus* had its beginnings at least as early as the Ballast Point Oligocene. It is here, as pointed out by Dall[3], more of an individual than a racial or specific character, but it is none the less present, and in any account of the canaliculate Fulgurs one must not fail to mention those Florida specimens which are provided with the shell structure in question. They are usually assigned (see A. N. S. P., No. 10,514) to *Fulgur spiniger* (Conrad), but their rather wide divergence from the type of that species is made evident by a com-

[1] It cannot be too strongly emphasized that the tabulated results are intended to apply only to those specimens which are regarded as *average*. In every race or species individuals may be selected which exhibit either more or less acceleration of shell characters than does the average example.

[2] In the diagrams the cancellated stage when known to be present is included with stage A.

[3] *Trans. Wagner Free Institute of Science of Phila.*, vol. III, pt. 1, p. 111.

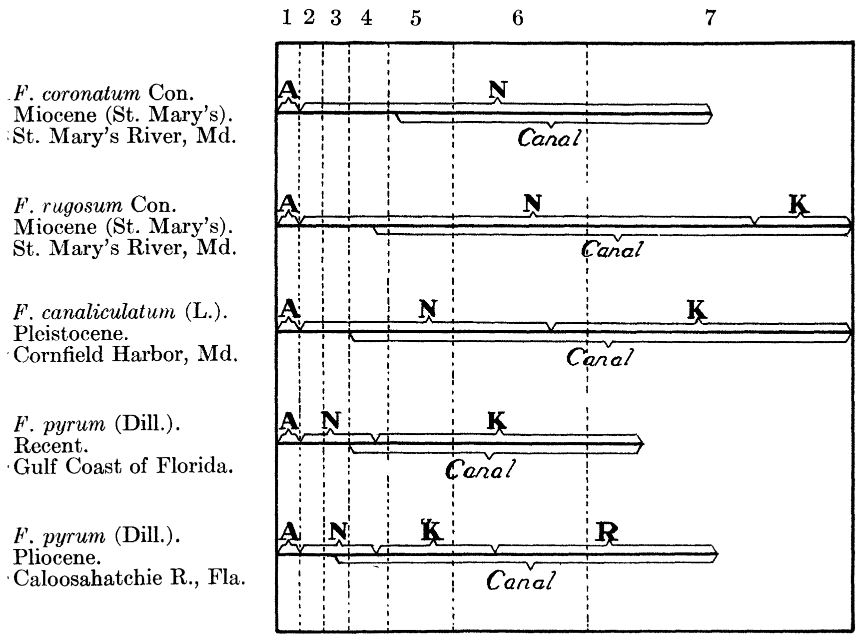

TABLE I.—The *coronatum-pyrum* Sequence.

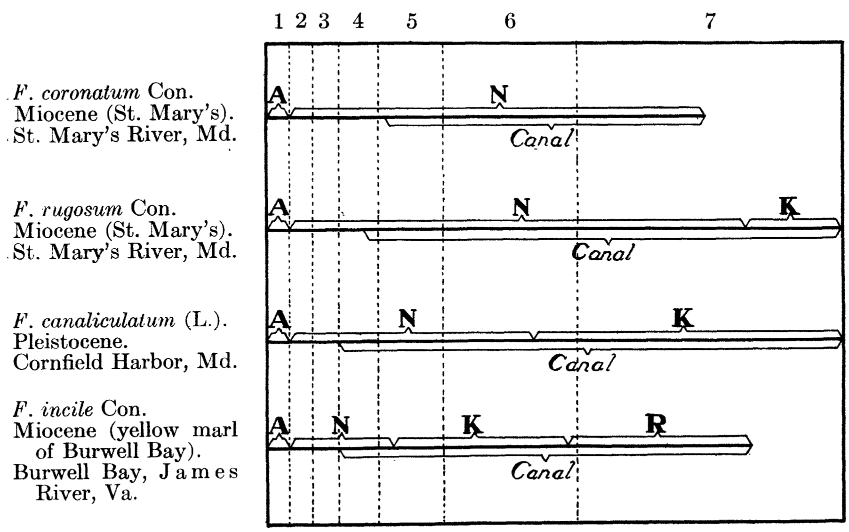

TABLE II.—The *coronatum-incile* Sequence.

parison with the figure which accompanies the original description.[4] They are without doubt a very primitive expression of the canaliculate type, but entire individuals of the series are all of small size, and the suspicion that they are not fully grown has prevented the author from including them in the tables with mature examples of other species. It is therefore considered better to begin the discussion of morphologic sequences with a later though perhaps equally primitive form—*Fulgur coronatum* Conrad[5]—from the St. Mary's Miocene.

The most striking sequence starting with this species terminates with a form from the Caloosahatchie Pliocene of Florida, which is usually included in *Fulgur pyrum* (Dillwyn). The steps in the sequence are *F. coronatum* Conrad (St. Mary's Miocene), *F. rugosum* Conrad[6] (St. Mary's Miocene), *F. canaliculatum* (L.)[7] (Maryland Pleistocene), *F. pyrum* (Dillwyn)[8] (Recent Florida), and *F. pyrum* (Dillwyn) (Florida Pliocene). These are all shown in Table I. Pleistocene specimens of *F. canaliculatum* have been selected because their preservation is superior to that of the available Recent specimens. It should also be noted that the ontogeny line which has been introduced for the Recent *F. pyrum* cannot be used to represent all individuals of the species.[9]

On consulting the table it will be seen that the sequence consists (1) in the progressively earlier appearance of the canal in passing from *F. coronatum* to the Caloosahatchie *F. pyrum*, (2) the progressive shortening of the noded stage through compression of the stage and acceleration of its later part, (3) the introduction and progressive acceleration of the keeled stage and its final compression in the terminal member of the sequence, and (4) the introduction of a final rounded stage in the Caloosahatchie *F. pyrum*[10] accompanied by compression and acceleration of the noded and keeled stages.

However little this arrangement may conform to geologic order or to one's ideas of phylogenetic relationship, it must be admitted that

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[4] *J. Acad. Nat. Sci. Phila.*, vol. 1, 2d ser., p. 117, pl. XI, fig. 32, 1848.

[5] "Fossils of the Medial Tertiary," pl. XLVI, fig. 1.
See also Md. Geol. Surv., Miocene, pl. XLVI, figs. 1*a*, 1*b*.

[6] "Fossils of the Medial Tertiary," pl. XLVI, fig. 4.
See also Md. Geol. Surv., Miocene, pl. XLVI, figs. 2*a*, 2*b*.

[7] See Md. Geol. Surv., Pliocene and Pleistocene, pls. XLVI, XLVII, XLVIII.

[8] "A Descriptive Catalogue of Recent Shells," L. W. Dillwyn, London, 1817, p. 485.
Martini Lister Syn. Method. Conch., 3d ed., 877, 1.
See also *Manual of Conchology*, G. W. Tryon, 1 ser., vol. III, pl. 58, figs. 402, 403.

[9] The suspicion is entertained that the Recent *F. pyrum* will eventually prove divisible into two species or at least races.

[10] This stage is also seen in many specimens of the Recent *F. pyrum*.

these forms just enumerated exhibit actual morphologic gradations. Any one feature is just a little stronger or more accelerated or perhaps just a little weaker in passing from *F. coronatum* to the Pliocene *F. pyrum*—in other words, the sequence is morphologic.

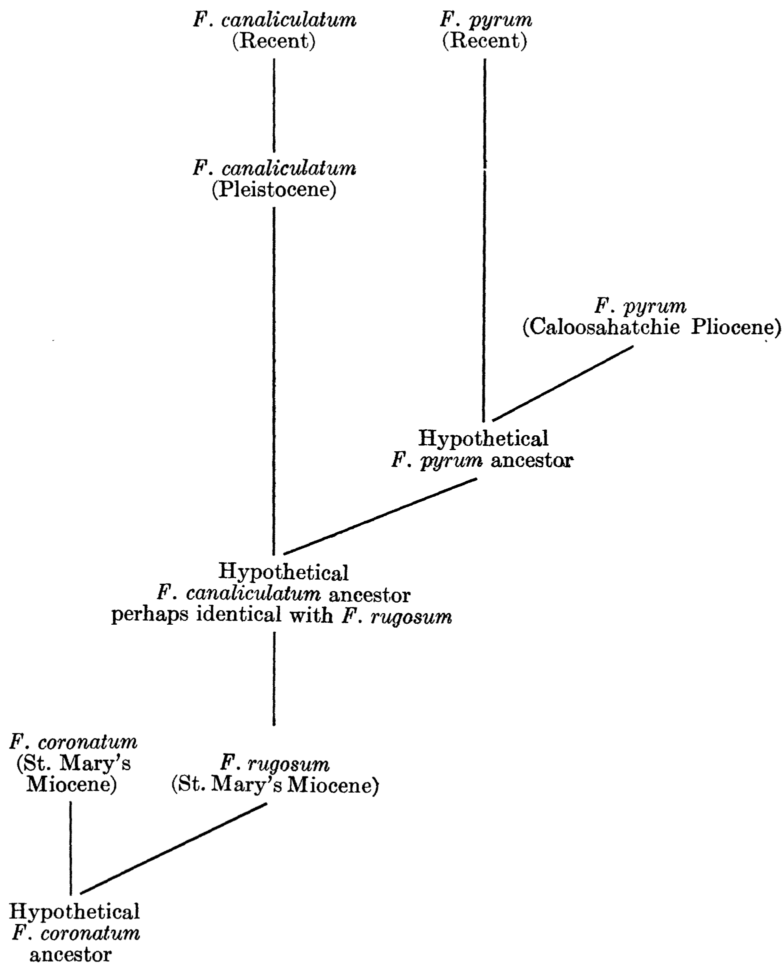
That the actual specimens from which these tabulated results were obtained could constitute part of a phylogenetic sequence is, of course, inadmissible. The specimens of *F. coronatum* and *F. rugosum* were contemporaries in the Miocene sea and the two lots of *F. pyrum* have their morphologic sequence the reverse of their geologic order. Again, *F. canaliculatum* and *F. pyrum* are contemporaries in the Recent seas and were probably even so in the Pliocene.

To interpret such data in terms of the phylogeny, one must decide between two quite diverse courses. In the first the worker may accept the geologic sequence as indicating the phylogeny and modify his ideas about organic evolution. The other course lies in choosing the morphologic sequence as portraying the phylogeny and introducing hypothetical species into the final scheme. In this latter case forms which are morphologically discordant but geologically intermediate must be regarded as intercalated migrants which have attained a high degree of specialization.

As an illustration of the difficulties presented by the first method of interpretation, attention is called to the Recent and Pliocene examples of *F. pyrum.* Those from the Pliocene are according to the morphology at the very limit of the sequence. If the Recent Florida individuals of this species are derived from the Caloosahatchie form, then the canal must have gone through a process the reverse of acceleration, and the disappearance or non-appearance of a final rounded stage must be accounted for in what is probably a majority of Recent examples. When the second method of interpretation is applied to these two assemblages, it is found necessary to derive both Recent and Pliocene examples from a hypothetical *F. pyrum* ancestor less specialized than the Pliocene form and not more specialized than the Recent form here tabulated. On this basis the Caloosahatchie *F. pyrum* is a terminal offshot which is extinct and not the ancestor of the less specialized Recent forms which are regarded as post-pliocene invaders from some other region.

At first glance it would appear that the method of interpreting by geologic position alone presents fewer difficulties. The study of these closely related species in this as well as in other groups of gastropods has, however, led the author to favor not the first, but the second method of interpreting. The reasons for choosing such

a course will be more fully discussed later and at present it is sufficient to say that the morphologic sequence displayed by *F. coronatum, F. rugosum, F. canaliculatum,* and the two assemblages of *F. pyrum* is believed to be best interpreted in terms of the phylogeny as follows:



F. rugosum has been reported from the Calvert and Choptank formations.[11] Both are older than the St. Mary's. As far as the

[11] Md. Geol. Surv. Miocene, p. 182.

writer has been able to learn, *F. coronatum* has not been found in these earlier beds. Those favoring purely stratigraphic methods will probably argue that, in any phylogenetic scheme, *F. coronatum* should be represented as derived from *F. rugosum*. This, however, would require an explanation of the absence of a keeled stage in *F. coronatum* and the acceptance of a theory that ontogenetic stages do sometimes go through a process the reverse of acceleration. The author inclines to the morphologic method in this case. It is believed that the derivation of *F. rugosum* from *F. coronatum* or something very close to it is amply justified, in spite of the fact that the latter form has not yet been proved to extend farther back than the St. Mary's Miocene.

In passing it may be said that the *F. pyrum*-like forms from the Duplin Miocene have been omitted purposely from the scheme, because of the suspicion, as yet unverified, that most museum sets are made up of specimens from more than one horizon in the Duplin beds.

The coronatum-incile Sequence.

The second morphologic sequence which commands our attention starts, as before, with *F. coronatum*, but ends with the late Miocene *F. incile* Conrad.[12] The gradations in this sequence, though not as complete as in the *F. coronatum-F. pyrum* sequence, are perhaps no less striking. Its members comprise *F. coronatum* Conrad (St. Mary's Miocene), *F. rugosum* Conrad (St. Mary's Miocene), *F. canaliculatum* (L.) (Pleistocene and Recent), and *F. incile* Conrad (Burwell Bay Miocene). These are shown in Table II. As before, the sequence consists (1) in the progressively earlier appearance of the canal in passing from *F. coronatum* to *F. incile;* (2) the progressive shortening of the noded stage through compression of the stage and acceleration of its later part; (3) the introduction and progressive acceleration of the keeled stage and its final compression in the terminal member, and (4) the introduction of a final rounded stage in *F. incile*.

In the succession of its ontogenetic stages, *F. incile* parallels *F. pyrum*, but in other respects it is quite different. In *F. pyrum* the tendency is for a shortening of the spire and a lengthening of the anterior canal. For *F. incile*, on the other hand, the reverse is true;

[12] "Descriptions of Miocene Shells of the Atlantic Slope," T. A. Conrad, *Am. J. Conch.*, p. 64, pl. 6, fig. 2, 1868.
See also *Am. J. Sci.*, vol. XXIII, p. 343.

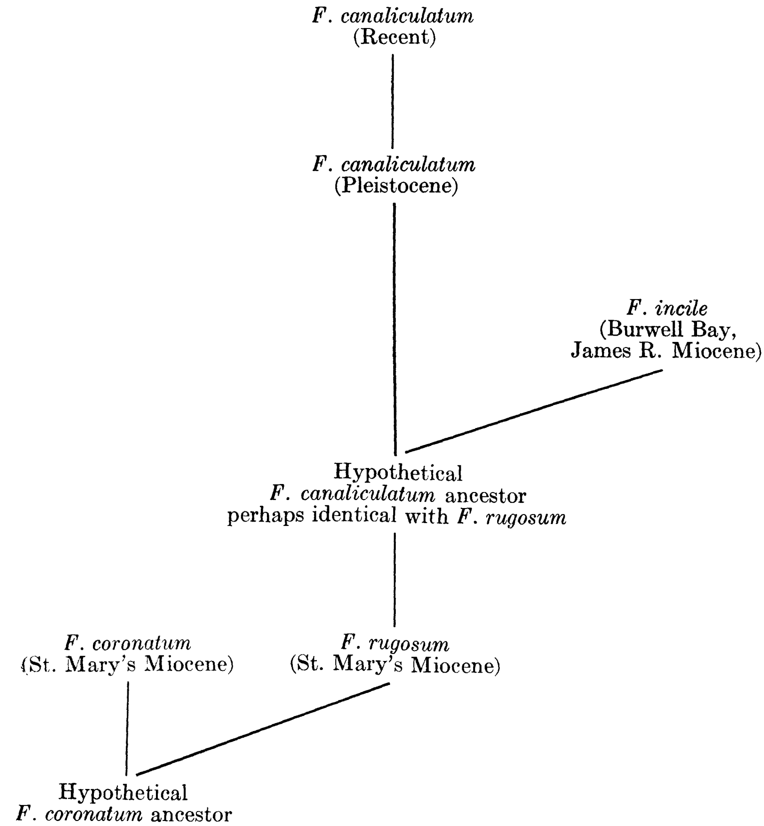
the canal shortening and the spire becoming more scalar during individual growth. Again the shell of *F. pyrum* tends to become light and thin, that of *F. incile* thick and heavy with the progress of the ontogeny.

The sequential relations presented by *F. canaliculatum* and *F. incile* are by no means apparent unless one is dealing with well-preserved specimens of the latter species. The average museum specimen of *F. incile* fails completely in this respect. If, however, the material is illustrative of the entire ontogeny, the similarity in the immature stages of these two species is very striking, and even the late whorls and short anterior siphon of *F. incile* are occasionally approached in very old and perhaps slightly abnormal individuals of *F. canaliculatum*.

When the geologic order of these species is considered in relation to their morphologic sequence, we are confronted with the fact that the Pleistocene and Recent (perhaps also Pliocene) *F. canaliculatum* is morphologically intermediate between *F. rugosum* of the St. Mary's Miocene and *F. incile* of the Burwell Bay (James River) Miocene. The descent of *F. incile* from any known race of *F. canaliculatum* is manifestly impossible, but the derivation of *F. canaliculatum* from *F. incile* could only be accomplished by the loss or non-development of acquired characters and a resumption of primitive features only slightly less marked than in *F. rugosum*.

Again, a decision must be made on what course to follow in interpreting the facts. We must either make the phylogeny agree with the stratigraphic order and modify our conception of the laws of evolution or else introduce a hypothetical common ancestor for both *F. canaliculatum* and *F. incile*. On this basis *F. incile* would be in no sense ancestral, but a terminal radiation of the late Miocene, which left no descendants.

In the case of the present sequence the author again favors the second method of interpretation and believes that the fewer difficulties are presented by the following phylogenetic scheme:



Geological Range and Classificatory Value of Shell Structures and Ontogenetic Stages.

Studies in evolution may be undertaken with the object of determining either the phylogeny of biologic groups, such as families, genera, species, or the phylogeny of organic structures. Though these two lines of research can never be regarded as entirely separate, they nevertheless constitute rather widely different aspects of the problem. Therefore, the results obtained in these present studies will be summarized with the view of emphasizing the phylogeny of structures.

The Sutural Canal:

(*a*) Oligocene to Recent.

(*b*) An ascendant character, becoming stronger and accelerating with the progress of time.

(*c*) Appearing in primitive forms of the Miocene after the beginning of the fifth whorl (*F. coronatum*).

(*d*) Appearing in a very specialized Pliocene form as early as the middle of the third whorl (*F. pyrum* Caloosahatchie Race).

(*e*) Though showing acceleration, its most notable changes are due to exaggeration of its depth or of its width.

(*f*) Its changes (variations or mutations) serve in part as a basis for the species of systematists. Its persistence is of generic or group value and serves to differentiate the canaliculate from the non-canaliculate Fulgurs.

The Noded Stage:

(*a*) Oligocene to Recent in this group.

(*b*) A declining character for this group, becoming weaker with the progress of time. Accelerating more by compression than by the dropping out of nodes.

(*c*) Appearing in all forms at about the beginning of whorl two. Closing the ontogeny of primitive forms of the Miocene (*F. coronatum*).

(*d*) Disappearing in very specialized forms before the completion of the fourth whorl (*F. pyrum*).

(*e*) Though its termination may show widely different degrees of acceleration, its most notable changes are due to its degeneration.

(*f*) Its changes through acceleration and degeneration serve in part as a basis for the species of systematists. Its persistence is of no higher classificatory value, for it is a primitive feature widely distributed among very diverse groups of marine gastropods.

The Keeled Stage:

(*a*) Miocene to Recent in this group.

(*b*) An ascendant character in the fairly primitive species (*F. rugosum*, *F. canaliculatum*). A declining character in the most specialized (*F. pyrum*, *F. incile*).

(*c*) Appearing in more primitive forms toward the end of the seventh whorl, in the most specialized toward the end of the fourth whorl.

(*d*) Terminating the ontogeny in fairly primitive forms (*F. rugosum*, *F. canaliculatum*). Ending early in the sixth whorl of the most specialized (*F. pyrum* Caloosahatchie Pliocene).

(*e*) Changes due to compression, acceleration, degeneration, and exaggeration are all well marked.

(*f*) Its changes through compression, acceleration, degeneration,

and exaggeration serve as a basis for the species of systematists. It has no higher classificatory value.

The Final Rounded Stage:

(*a*) Late Miocene to Recent in this group.

(*b*) An ascendant character appearing only in the most specialized species (*F. pyrum*, *F. incile*). Never a declining character, though it may perhaps be indicative of decadence.

(*c*) Never appearing in primitive forms. Appearing early in the sixth whorl of the most specialized form (*F. pyrum* Caloosahatchie Pliocene). Never, in this group, followed by any other ontogenetic stage.

(*e*) Its chief changes are due to its degree of exaggeration.

(*f*) Its changes through exaggeration help to serve as a basis for the species of systematists. It has no higher classificatory value.

In the preparation of these notes the collections most extensively studied were those of The Academy of Natural Sciences of Philadelphia and of the Wagner Free Institute of Science of Philadelphia. Acknowledgments are due to the officers of these institutions for many courtesies and to Mrs. Ethel Ostrander Smith for the careful execution of the drawings.

Explanation of Plate XXIV.

Fig. 1.—*Fulgur coronatum* Conrad. Miocene (St. Mary's). St. Mary's River, Md. Apical view of an adult individual of about 6½ whorls. Illustrates a rather primitive type of the sutural canal and a vigorous noded stage which persists to the end of the ontogeny. Diameter of last whorl at shoulder = 79 mm.

Fig. 1*a*.—Side view of specimen shown in fig. 1.

Fig. 2.—*Fulgur rugosum* Conrad. Miocene (St. Mary's). St. Mary's River, Md. Apical view of an adult individual of about 7 whorls. Shows a well-developed sutural canal and a degenerating noded stage with its gradual transition into a keeled stage toward the end of the seventh whorl. Diameter of last whorl at shoulder = 100 mm.

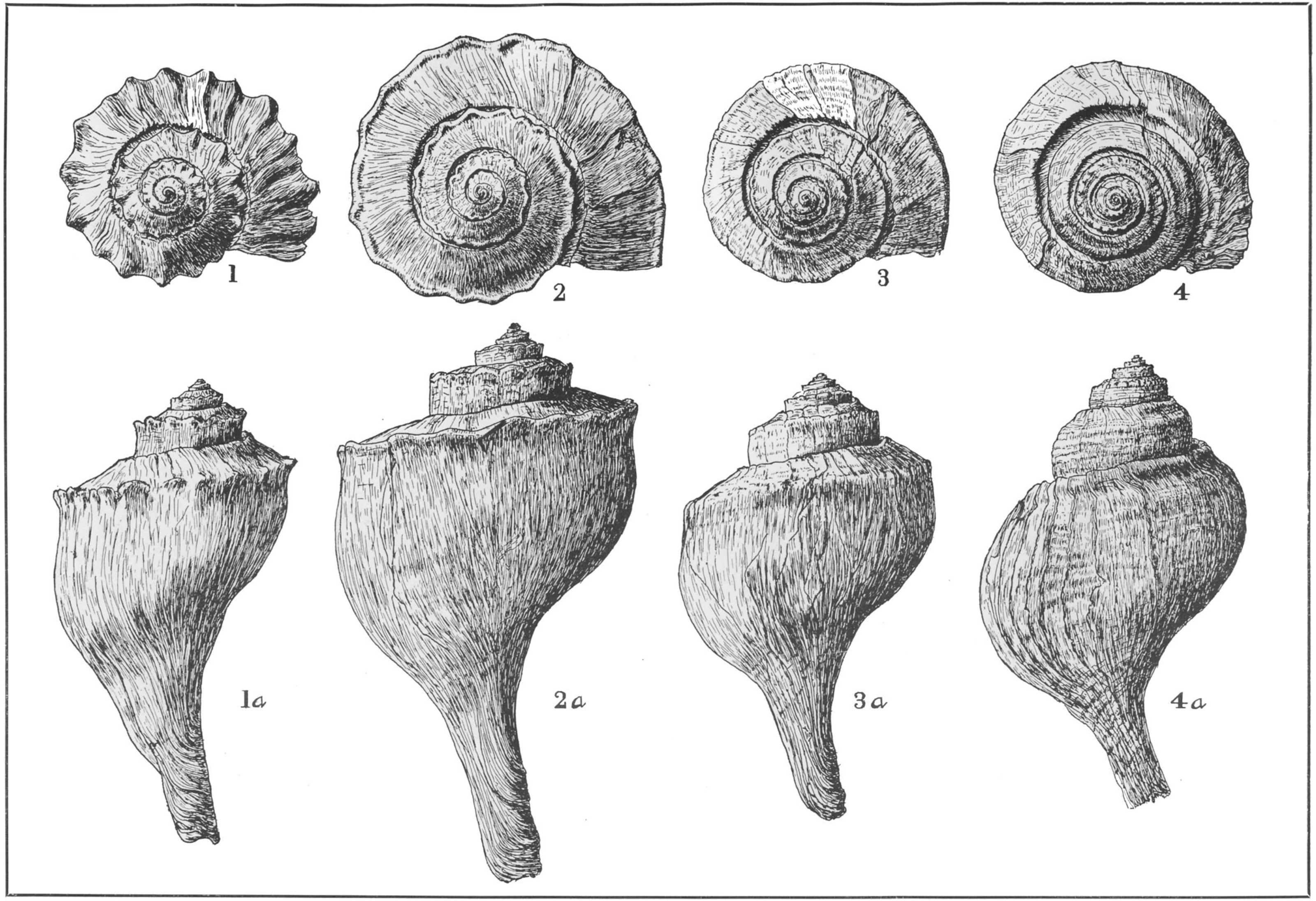
Fig. 2*a*.—Side view of specimen shown in fig. 2.

Fig. 3.—*Fulgur canaliculatum* (L.). Recent. Apical view of an immature individual of about 6¾ whorls. Shows a well-developed sutural canal and an accelerated and degenerate noded stage, which passes into a keeled stage toward the end of the sixth whorl. Diameter of last whorl at shoulder = 67 mm.

Fig. 3*a*.—Side view of specimen shown in fig. 3.

Fig. 4.—*Fulgur incile* Conrad. Late Miocene. Yellow marl of Burwell Bay, James River, Va. Apical view of nearly mature individual of 6¾ whorls. Shows a highly developed sutural canal, a much accelerated and compressed noded stage, and an accelerated and compressed keeled stage which passes into a final rounded stage toward the end of the sixth whorl. Diameter of last whorl = 81 mm.

Fig. 4*a*.—Side view of specimen shown in fig. 4.



BURNETT SMITH: MORPHOLOGIC SEQUENCE IN FULGUR.